

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
PROCECIDOCHARES ANTHRACINA (DOANE) (DIPTERA: TEPHRITIDAE)
ON *SOLIDAGO CALIFORNICA* NUTTALL IN SOUTHERN CALIFORNIA**

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Abstract.—*Procecidochares anthracina* (Doane) is a univoltine, circumnatal, tephritid fly widely distributed in the western United States and apparently nearly monophagous on *Solidago californica* Nuttall and as yet unknown congeners probably of similar growth habit. Unique among other *Procecidochares* species studied to date, *P. anthracina* reproduces gregariously in underground bud galls on shoots arising from host-plant rhizomes. The egg, first through third instars, and puparium are described and figured for the first time. The small, rounded, rugose pads that circumscribe the prothorax; the presence of four, small subdorsal sensilla ventrolaterad of the dorsal sensory organ and dorsal to the anterior sensory lobe, and the lateral spiracular complexes distinguish the third instar from other gallicolous *Procecidochares* examined to date. Pupariation occurs within subsurface galls and teneral adults must climb upward through several cm of humus to free themselves and mate. Premating, mating, and postmating behaviors are described which include spurts of exceptionally rapid, blurred wing enantiations. Mated females must reenter the humus layer to oviposit in buds on buried shoots, as subsequently must parasitoids to locate and probably enter galls to oviposit in the larvae or puparia. *Eurytoma obtusiventris* Gahan (Hymenoptera: Eurytomidae) is reported as a solitary, larval-pupal endoparasitoid reared from puparia; *Pronotalia carlinarium* Gradwell (Hymenoptera: Eulophidae) is a gregarious endoparasitoid of puparia.

Key Words: Insecta, *Procecidochares*, *Solidago*, biology, galls, taxonomy of immature stages, reproductive behavior, parasitoids

Life histories and immature stages of four species of *Procecidochares* (Diptera: Tephritidae) in southern California have been described to date, i.e. *P. flavipes* Aldrich (Goeden et al. 1994a), *P. kristineae* Goeden (Silverman and Goeden 1980, Goeden and Teerink 1997), *P. lisae* Goeden (Goeden and Teerink 1997), and *P. stonei* Blanc and Foote (Green et al. 1993). Herein we describe the life history and immature stages of a fifth species, *P. anthracina* (Doane), which uniquely forms bud galls on shoots arising from subsurface rhizomes of *Solidago californica* Nuttall (Asteraceae).

MATERIALS AND METHODS

Our field studies on *P. anthracina* were conducted principally at two locations in southern California during 1992–1995: (1) at the junction of Kitchen Creek Road and the Sunrise Highway at 1720-m elevation, Cleveland National Forest, San Diego Co. and (2) in Spilman Canyon SE of Lake Hemet at 1380 m, San Bernardino National Forest (S section), Riverside Co. Infested rootstocks dug from humus beneath deciduous oaks (*Quercus* spp.) within patches of shoots of *Solidago californica* were transported in cold-chests in an air-conditioned

vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty six eggs dissected from buds and seven first-, 12 second-, and 14 third-instar larvae, and six puparia from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia obtained from galls were individually caged with excavated rhizome fragments attached or unattached to basal portions of aerial shoots in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. Those cagings without rhizome bouquets were used for longevity studies and those with bouquets for oviposition tests in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991) for direct observations, videorecording, and still-photography of their courtship and copulation behavior.

Plant names used in this paper follow Munz (1974); tephritid names and nomenclature follow Foote et al. (1993). Terminology and telegraphic format used to de-

scribe the immature stages follow Goeden et al. (1993; 1994a, b; 1995a, b) and Goeden and Teerink (1996a, b, c; 1997) and our earlier works cited therein. Means $\pm$ SE are used throughout this paper. Voucher specimens of *P. anthracina* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—First described by Doane (1899) as *Oedaspis anthracina*, then transferred to *Cecidochares* by Bezzi (1910), *P. anthracina* was assigned its current name by Bezzi and Tavares (1916) (Foote et al. 1993). Only the wing pattern of the adult has been figured by Doane (1899), Foote and Blanc (1963), and Foote et al. (1993). Adults are separated from other congeners, and ultimately from *P. australis* Aldrich and *P. grindeliae* Aldrich, which this species most closely resembles, by the characters incorporated in the key to North American *Procecidochares* in Foote et al. (1993).

Immature stages.—**Egg:** Twenty eggs of *P. anthracina* were white, opaque, smooth; with an elongate-ellipsoidal body, 0.51 ± 0.005 (range, 0.47–0.54) mm long, 0.14 ± 0.002 (range, 0.13–0.19) mm wide, smoothly rounded at tapered posterior end (Fig. 1A), and with a peg-like anterior pedicel, 0.02 mm long and a few, large aeropyles (Fig. 1B). The egg of *P. anthracina* is similar in shape but smaller than *P. flavipes* (Goeden et al. 1994a) and *P. lisae* (Goeden and Teerink 1997). *Procecidochares stonei* (Green et al. 1993) and *P. kristineae* (Silverman and Goeden 1980, Goeden and Teerink 1997) eggs are smaller than *P. anthracina* eggs and have a tapered pedicel with much smaller, oval aeropyles.

Third instar: Third instar of *P. anthracina* superficially smooth, elongate cylindrical, tapering anteriorly, rounded posteriorly (Fig. 2A); gnathocephalon conical,

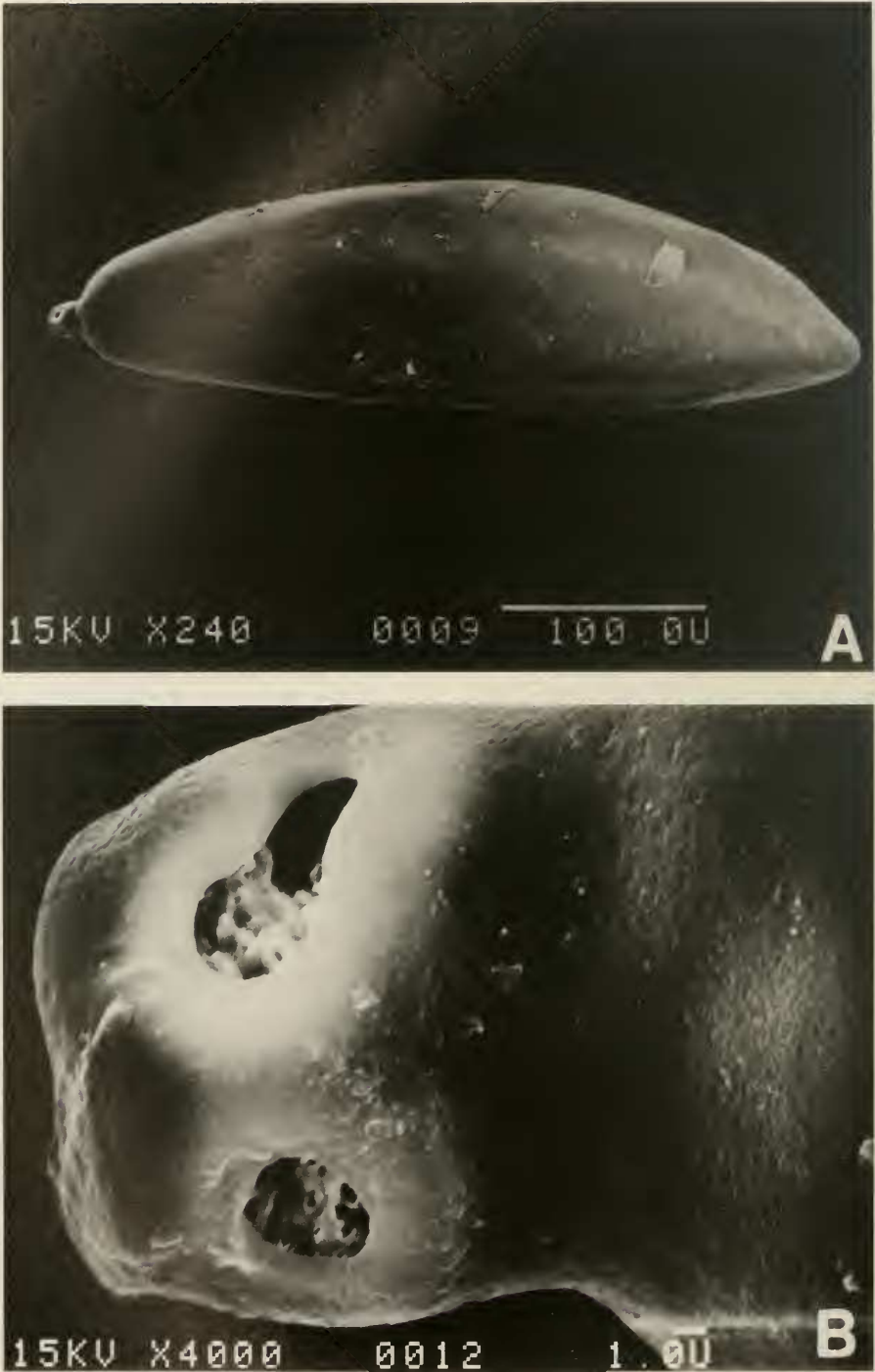


Fig. 1. Egg of *Procecidochares anthracina*. (A) habitus; (B) anterior end, aeropyles.

smooth, lacking rugose pads (Fig. 2B); paired dorsal sensory organs consist of a dome-shaped papilla (Fig. 2C-1); four, small, dome-shaped sensilla, each with a central papilla, located ventrolaterad of dorsal sensory organ (Fig. 2C-2); anterior sensory lobe bears the terminal sensory organ (Fig. 2C-3), pit sensory organ (Fig. 2C-4), lateral sensory organ (Fig. 2C-5) and supralateral sensory organ (Fig. 2C-6); stomal sense organs distinct, composed of raised lobe with two pore sensilla, ventrad of anterior sensory lobes (Fig. 2D-1); lateral sensilla laterad of stomal sense organ (Fig. 2D-2), two of eight verruciform sensilla, including ventrolateral sensilla, circumscribing gnathocephalon (Fig. 2B-1); mouth hooks tridentate, teeth conical (Fig. 2B-2, D-3); median oral lobe obscured in prepared specimens; prothorax covered anteriorly with small, rounded rugose pads (Fig. 2B-3); verruciform sensilla posterior to rugose pads on dorsal half of prothorax (Fig. 2B-4); anterior spiracles on posterior margin of prothorax consist of two dome-shaped papillae (Fig. 2E); meso- and metathoracic lateral spiracular complexes consist of an open spiracle and two verruciform sensilla; abdominal lateral spiracular complexes with an open spiracle (Fig. 2F-1) and one verruciform sensillum (Fig. 2F-2); caudal segment smooth (Fig. 2G-1); posterior spiracular plates with three ovoid rimae, ca. 0.03 mm in length (Fig. 2H-1), and four spiniform interspiracular processes, longest measuring 0.007 mm (Fig. 2H-2); compound sensilla ventrad of posterior spiracular plates consist of a stelex sensillum (Fig. 2G-2) and a verruciform sensillum (Fig. 2G-3).

The *P. anthracina* third instar differs from that of the flower head-infesting *P. flavipes* in that the mouth hooks are tridentate, the rugose pads are limited to the prothorax and no minute acanthae are present in the intersegmental areas nor on the caudal segment (Goeden et al. 1994a). *Procecidochares anthracina* more closely resembles the other gall-forming *Procecidochar-*

es spp. we previously have examined, i.e., *P. kristineae*, *P. lisae* and *P. stonei*, but differs mainly in that its prothorax is circumscribed by small, rounded rugose pads; whereas, the other three gall-forming species lack these rugose pads (Goeden and Teerink 1997; Green et al. 1993). Differences also were noted in the lateral spiracular complexes; whereby, *P. kristineae* and *P. lisae* lack verruciform sensilla on the metathorax (Goeden and Teerink 1997), and the verruciform sensilla in *P. stonei* are anterior to the spiracle (Green et al. 1993). Several previously undescribed sensilla were found on the gnathocephalon of *P. anthracina*. Four small sensilla located ventrolaterad of the dorsal sensory organ and dorsad to the anterior sensory lobe are collectively named subdorsal sensilla, and are unreported among previously examined, nonfrugivorous Tephritidae (Goeden and Headrick 1990, 1991a, b, 1992; Goeden et al. 1993, 1994a, b, 1995a, b; Goeden and Teerink 1996a, b, c; Green et al. 1993; Headrick and Goeden 1990, 1991, 1993; Headrick et al. 1995). A single, subdorsal sensillum located laterad to the dorsal sensory organ was reported in *Trupanea nigricornis* and *T. bisetosa* (Knio et al. 1996) and *Dioxyna picciola* (Headrick et al. 1996).

Second instar: Second instar of *P. anthracina* superficially smooth, elongate cylindrical (Fig. 3A); gnathocephalon conical, smooth, lacking rugose pads (Fig. 3B); paired dorsal sensory organs each consist of a dome-shaped papilla (Fig. 3C-1); anterior sensory lobes (Fig. 3B-1) bear the terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); stomal sense organ ventrad of anterior sensory lobe (Fig. 3B-2); mouth hooks obscured, apical tooth conical (Fig. 3B-3); median oral lobe obscured in prepared specimens; prothorax covered anteriorly with small, rounded rugose pads; verruciform sensilla posterior to rugose pads on dorsal half of prothorax; anterior spiracles

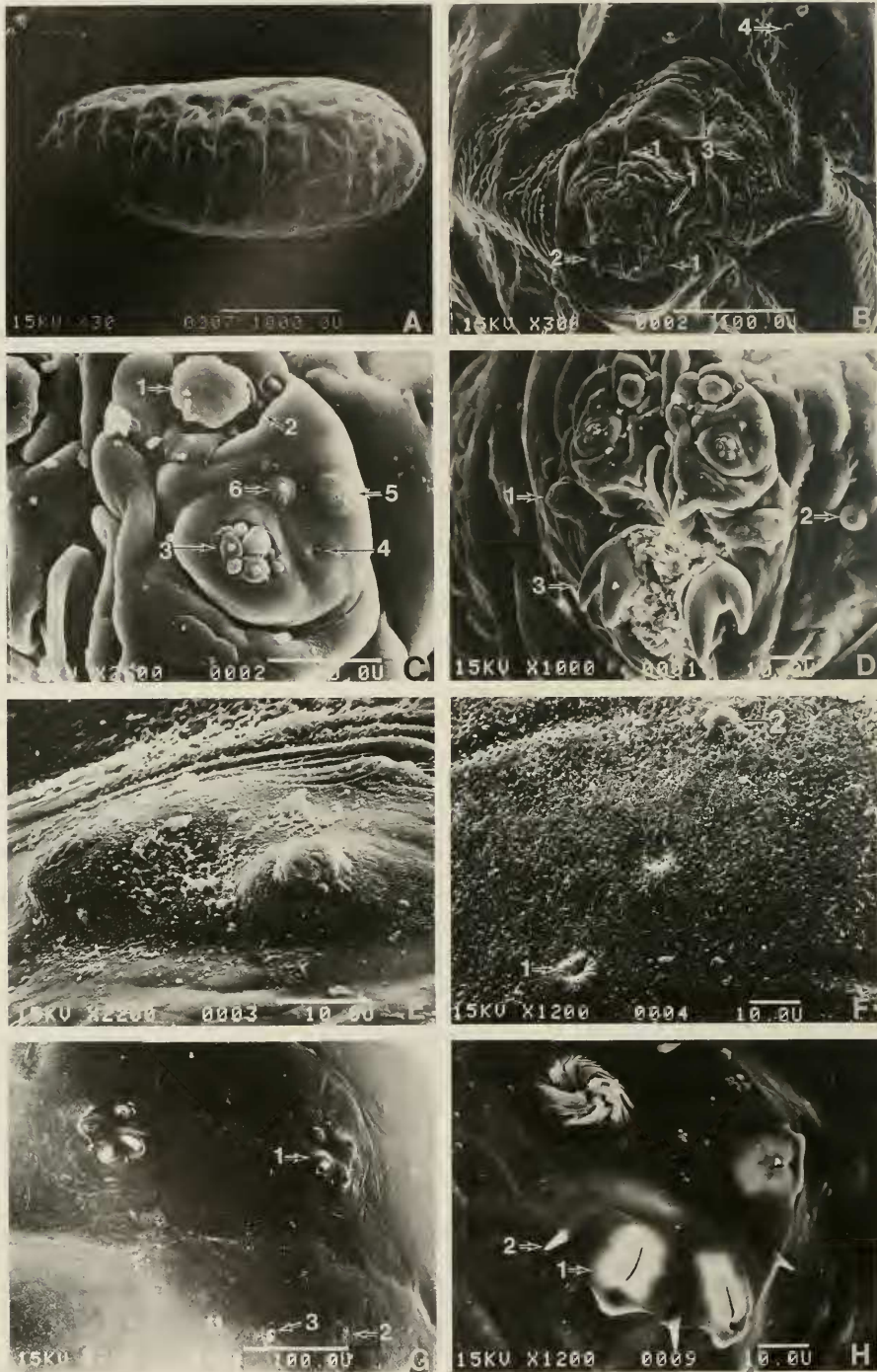


Fig. 2. Third instar of *Procecidochares anthracina*. (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—verruciform sensilla, 2—mouth hooks, 3—rugose pads, 4—prothoracic verruciform sensilla; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—subdorsal sensilla, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ; (D) gnathocephalon, anterior view, 1—stomal sense organ, 2—lateral sensillum, 3—mouth hooks; (E) anterior spiracles; (F) fourth abdominal lateral spiracular

each consist of two dome-shaped papillae; lateral spiracular complexes not observed; caudal segment circumscribed by stelex sensilla (Fig. 3D-1); posterior spiracular plates bear three ovoid rimae, ca. 0.008 mm in length (Fig. 3D-2), and four spiniform interspiracular processes, longest measuring 0.005 mm (Fig. 3D-3); compound sensilla ventrad of spiracular plates consist of a stelex sensillum (Fig. 3D-4) and a verruciform sensillum (Fig. 3D-5).

Second instars of *P. anthracina* possess the same sensory structures as the mature larva, but the structures are not as well-defined. The mouth hooks, median oral lobe, and lateral spiracular complexes were obscured in prepared specimens.

First instar: First instars of *P. anthracina* cylindrical, rounded posteriorly, minute acanthae circumscribe segmental lines (Fig. 4A); gnathocephalon conical, smooth (Fig. 4B); dorsal sensory organ consists of dome-shaped papilla (Fig. 4B-1, C-1); anterior sensory lobe (Fig. 4B-2) bears terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4) and supralateral sensory organ (Fig. 4C-5); stomal sense organs ventrad of anterior sensory lobes indistinct (Fig. 4B-3); mouth hooks obscured in prepared specimens; anterior spiracles absent; lateral spiracular complexes not observed; caudal segment circumscribed by stelex sensilla (Fig. 4D-1); posterior spiracular plates bear two ovoid rimae, ca. 0.001 mm in length (Fig. 4D-2), and four rudimentary interspiracular processes, ca. 0.0003 mm in length (Fig. 4D-3).

The features of the first instar are less distinct than those of the mature larva. The first instar lacks the prothoracic rugose pads, but does have minute acanthae circumscribing the intersegmental lines not

found in later instars. The anterior sensory lobes and dorsal sensory organs comprise most of the gnathocephalon. The four subdorsal sensilla are not present in the first instar. As the mouth hooks were obscured in all prepared specimens, we were unable to determine if the apical tooth was grooved as in *P. lisae* and *P. kristineae* (Goeden and Teerink, 1997). The respiratory system of the first instar was very reduced compared to both later instars. The posterior spiracular plates with two small rimae and the interspiracular processes were almost indistinct.

Puparium: Puparium of *P. anthracina* elongate ellipsoidal (Fig. 5A), anterior end bears the invagination scar (Fig. 5A-1), prothoracic rugose pads (Fig. 5B-2), verruciform sensilla (Fig. 5B-3) and anterior spiracles (Fig. 5B-4); caudal segment smooth, bears the posterior spiracular plates (Fig. 5C-1), and compound sensilla (Fig. 5C-2). One hundred and forty five puparia of *P. anthracina* averaged 3.56 ± 0.03 (range, 2.16–4.68) mm in length; 1.55 ± 0.02 (range, 0.94–1.99) mm in width.

DISTRIBUTION AND HOSTS

Because of its unusual reproduction on subsurface rootstocks and its widespread distribution in the western United States (Foote et al. 1993), where alternate hosts other than *S. californica* must occur, we believe that *P. anthracina* probably is nearly monophagous on *Solidago* spp. of similar growth habit. This assessment of its host affinities discounts the published “unpublished record” for an unidentified species of *Erigeron* in Wasbauer (1972) cited by Foote et al. (1993). *Erigeron* belongs to a different subtribe, Asterinae, of the tribe Solidagininae, than *Solidago* (Bremer 1994). Foote and Blanc (1963) reported a sweep

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complex, 1—spiracle, 2—verruciform sensillum; (G) caudal segment, 1—posterior spiracular plates, 2—compound sensillum, stelex sensillum, 3—compound sensillum, verruciform sensillum; (H) posterior spiracular plate, 1—rima, 2—interspiracular process.

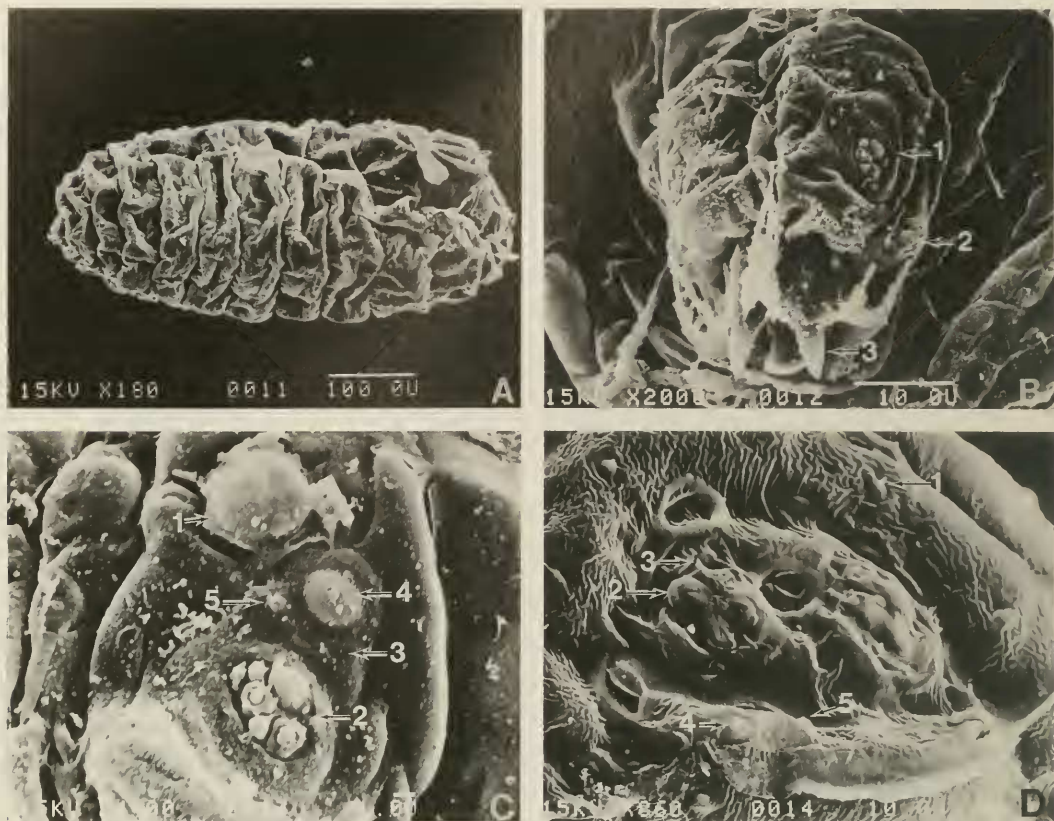


Fig. 3. Second instar of *Procecidochares anthracina*. (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—anterior sensory lobe, 2—stomal sense organ, 3—mouth hooks; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) caudal segment, 1—stelex sensillum, 2—rima, 3—interspiracular process, 4—compound sensillum, stelex sensillum, 5—compound sensillum, verruciform sensillum.

record from a *Chrysothamnus* sp., but that plant is a doubtful host of *P. anthracina*. Sweep records of adults all too often are misleading and suspect indicators of the host-plant affinities of nonfrugivorous tephritids. All four species of *Procecidochares* from southern California previously studied in similar detail as *P. anthracina* (Silverman and Goeden 1980, Green et al. 1993, Goeden et al. 1994a, Goeden and Teerink 1997) are strictly monophagous or nearly monophagous on congeneric hosts.

BIOLOGY

Egg.—Galls of *P. anthracina* were found on shoots arising from rhizomes of *Solidago californica* under crowns of decidu-

ous oaks within a 3- to 10-cm deep surface layer of humus, i.e., decayed leaves, twigs, branches, and acorns; therefore, females must penetrate this loosely packed organic layer to reach the buried axillary buds within which the eggs are deposited (Fig. 6A, B). This behavior would require that females climb down the buried parts of vertical aerial shoots, or buried tree trunks, near to which galls most commonly were found. Females apparently may also follow farther along the horizontal rhizomes at the humus/mineral-soil interface and climb one or more vertical subsurface shoots to oviposit in the axillary buds. Alternatively, the females may sense and reach these buried shoots by penetrating the humus from di-

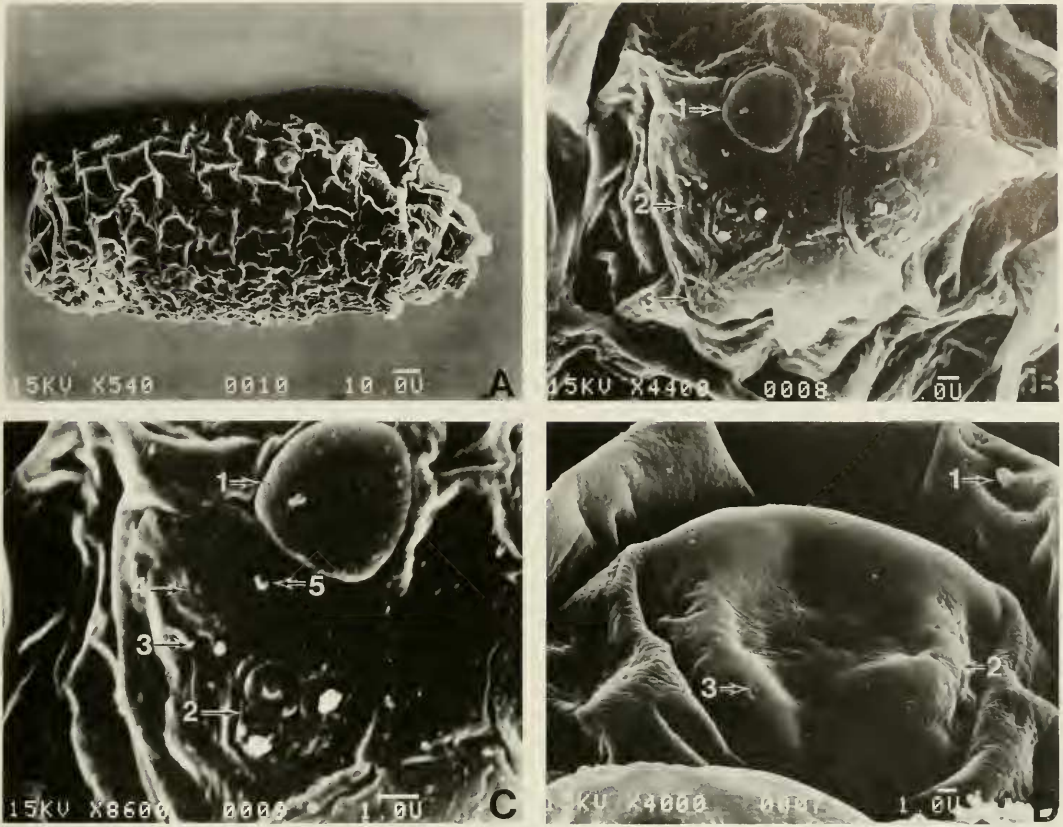


Fig. 4. First instar of *Procecidochares anthracina*. (A) habitus, anterior to right; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) caudal segment, 1—stelex sensillum, 2—rima, 3—interspiracular process.

rectly above (like a pig rooting for truffles), but this preovipositional searching behavior seems less certain than using shoots and rhizomes as pathways. Ovipositing adults never were observed in nature, only in insectary cages (Fig. 6A).

The eggs were inserted pedicel upward, side-by-side, and lengthwise in bands within a prominent axillary bud, but not penetrating any tissue. Instead, the eggs were laid parallel to the long axis of the bud and stem, between an outer bract and bud, between the bud and stem, or among the leaf primordia (Fig. 6B). As many as 16 eggs were found in a single bud in nature; whereas, as many as 18 eggs were laid by one female in 1 day in an axillary bud in insectary cagings (Fig. 6A, B).

Larva.—Eggs hatch about a week after their deposition (Silverman and Goeden 1980, Green et al. 1993), but then the first instars persist, as these and later instars develop slowly through the fall, winter, and spring. The first instars initially develop gregariously by feeding within axils and buds in shallow, linear, surface scars (Fig. 6C). Some first instars move to adjacent axillary buds on the same shoot; others remain behind and feed gregariously within the original bud or divide into subgroups that subsequently each form separate galls that may arise from one axillary bud. Gall formation appears to result from larval activities, not maternal stimuli, as bud and stem swelling begins only after the larvae begin their surface feeding. Multiple gall

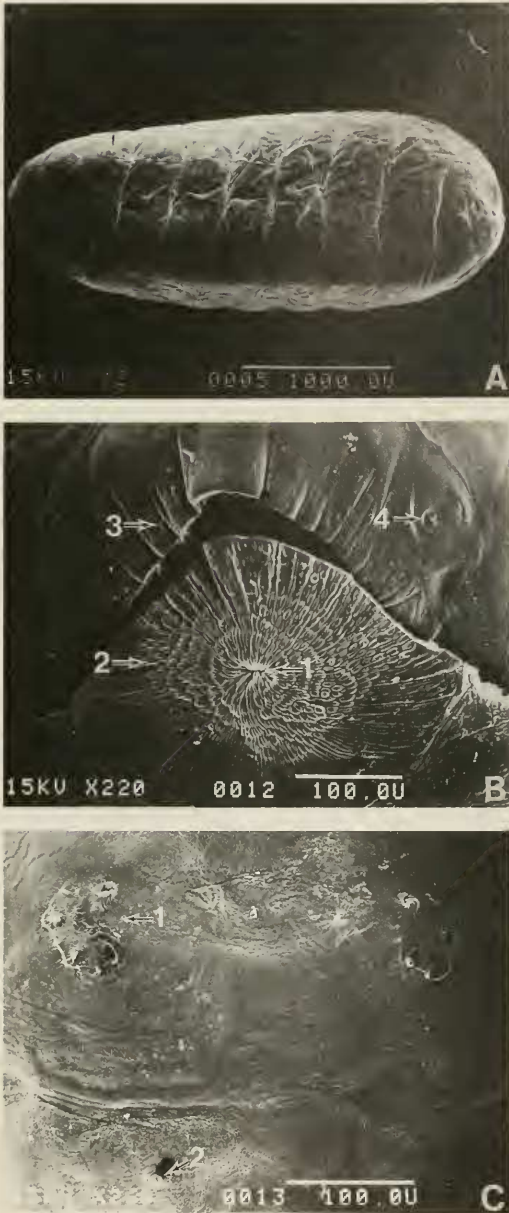


Fig. 5. Puparium of *Procecidochares anthracina*. (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—prothoracic rugose pads, 3—prothoracic verruciform sensilla, 4—anterior spiracles; (C) caudal segment, 1—posterior spiracular plates, 2—compound sensillum.

formation from single aerial axillary buds also was reported for *P. kristinae* and *P. liseae* (Goeden and Teerink 1997).

Examination of 140 shoots on rhizome

fragments excavated at study site 1 on 8.xii.1994, yielded seven shoots (5%) an average of 10.2 ± 0.6 (range, 1.9–23) mm in length that together bore 14 axillary buds and 16 ± 2.5 (range 7–25) early first instars per shoot. These infested axillary buds averaged 0.56 ± 0.06 (range, 0.37–1.12) mm in length by 0.42 ± 0.04 (range, 0.18–0.84) mm in width and each contained an average of 6 ± 1.0 (range, 1–16) early first instars (Fig. 6C). Infested buds were located an average of 3.9 ± 0.6 (range, 1.8–8.0) mm below the shoot apices (Fig. 6D).

Five infested shoots on five separate rhizome fragments excavated at the same site on 2.ii.1995 each bore an average of 14 ± 2 (range, 9–20) late first instars, or an average of 6 ± 1.4 (range, 3–10) larvae per axillary bud. The swollen axillary buds (incipient galls) measured 2.56 ± 0.67 (range, 0.74–4.56) mm long by 1.63 ± 0.35 (range, 0.74–2.56) mm wide and contained subspheroidal, open central cavities 0.2–0.4 mm in diameter (Fig. 6E). These incipient galls were borne on shoots that averaged 9.4 ± 1.4 (range, 6.6–13.7) mm in length (Fig. 6D).

The only galls found containing second instars were five in a sample collected at site 1 on 28.iii.1994. The subspheroidal galls contained an average of 4 ± 1 (range, 2–8) second instars and averaged 3.9 ± 1.4 (range, 1.5–9.1) mm in length by 5.9 ± 2.0 (range, 1.9–10) mm wide. Each gall contained a central cavity 1.1–4.0 mm in diameter and had walls 1.6 ± 0.2 (range, 1.3–2.6) mm thick (Fig. 6F).

Galls containing third instars, or sometimes third instars and puparia (Fig. 6H), were sampled more frequently than those containing the first two instars at both study sites. Twenty clusters of full-size galls as shown in Fig. 6G contained an average of 6 ± 1 (range, 1–14) galls and an average total of 12 ± 2 (range, 2–43) third instars per shoot. These galls were subspheroidal, ovoidal, or obclavoidal in shape and pale violet basally, whitish medially, and pale green or white apically (Fig. 6G). Forty-



Fig. 6. Life stages of *Procecidochares anthracina* on *Solidago californica*. (A) ovipositing female, (B) axillary bud on shoot with bracts removed to show newly deposited eggs (arrows), (C) first instar larvae (arrows) feeding gregariously on shoot stem (line = 0.1 mm), (D) galled axillary bud on stalk of shoot dug from humus, (E) sagittal section of gall containing second instars (arrows), (F) sagittal section of gall containing early third instars, (G) cluster of full-size galls, (H) sagittal section through full-size gall containing third instars and puparia, and (I) full-size gall showing exit channel and empty puparia. Lines = 1 mm, except as noted.

four (54%) of 81 galls with third instars were borne on pedicels or stalks 7.7 ± 1.0 (range, 2–34) mm in length; the remainder (46%) were sessile on shoots. The 81 galls averaged 13.3 ± 0.3 (range, 8–20) mm in length and 8.0 ± 0.2 (range, 3.1–12) mm in width. Each gall contained an average of 3 ± 0.2 (range, 1–10) third instars within a subspheroidal, ovoidal, or obovoidal, open central cavity, which averaged 6.06 ± 0.20 (range, 1.84–10.64) mm in length and 3.81 ± 0.12 (range, 1.68–6.72) mm in width. Eighteen (22%) of these galls also bore an average of 2 ± 0.4 (range, 1–7) puparia indicating differential rates of development within galls. Another 145 galls were examined that only contained an average of 5 ± 0.4 (range, 1–21) empty (Fig. 6I) or still intact puparia.

Adult.—Eclosing adults emerge through a common, open exit channel at the apex of each gall, past and through an encircling whorl of bracts, and continue upward through the humus to reach the surface. Adults were relatively long lived among gallicolous congeners studied in southern California to date (Silverman and Goeden 1980, Green et al. 1993, Goeden and Teerink 1997). Twenty seven males lived an average of 47 ± 3 (range, 14–70) days in insectary cagings; 19 females averaged 38 ± 3 (range, 14–62) days. Females (Fig. 7A) are sexually immature at emergence ($n = 3$), but within a week produce a full complement of mature ova ($n = 3$), apparently mainly from tiny fat bodies (globules) observed in the haemolymph of newly emerged flies, which disappear during oviogenesis. In laboratory arenas, males 1–18 days old and females 1–22 days old mated (Fig. 7B, C), but this behavior, like oviposition, never was observed in nature nor were free-living adults ever collected.

The adults exhibited reproductive behavior typical of other circumnata, gallicolous species of *Procecidochares* studied in southern California, i.e., a lack of courtship behavior, the exhibition of enantion type wing movements by both sexes, and male

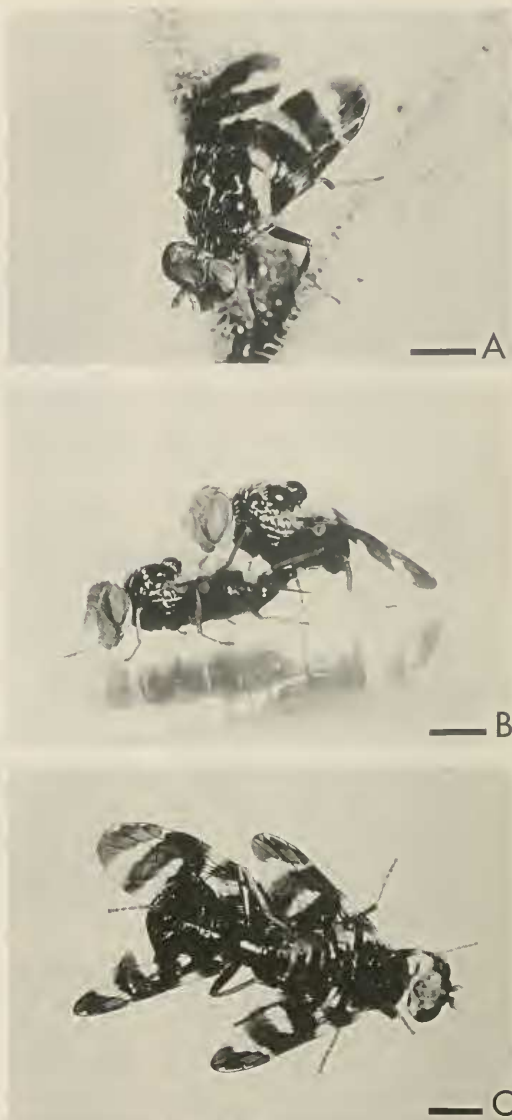


Fig. 7. *Procecidochares anthracina*. (A) dorsal view of female, (B) mating pair, lateral view, (C) Mating pair, ventral view. Lines = 1 mm.

stalking of females prior to mating (Green et al. 1993, Headrick and Goeden 1994); however, they also displayed several unique behaviors in oviposition cages and petri dish arenas. For example, females displayed rapid enantion in brief spurts, two or three times per second after they alternately or synchronously supinated their wings through arcs of 20–30° as they briefly

paused while walking along caged shoots between ovipositions, or while resting after ovipositing. So rapid was this enantion that the wings became blurred. Four females climbed atop prominent buds on excised shoots during oviposition in cages, recurved their abdomens, and inserted their aculei between bracts for an average of 6 ± 2 (range, 3–12) minutes, taking about 2 minutes to lay a single egg (Fig. 6A).

Both sexes displayed wing supination blending into rapid wing enantion while tracking each other in arenas prior to copulation, or rapid enantion during copulation if agitated, especially the females, just prior to and following postcopulatory separation. Twenty seven copulations averaged 63 ± 6 (range 25–148) minutes in duration and occurred throughout the day, but mostly at dusk. Males dismounted females either by walking forward over the head of the females or by stepping off to one side of her as she turned 180° , and they continued walking in opposite directions, as the male's genitalia was pulled free; the entire process lasted only a few seconds to as long as 20 seconds ($n = 4$). The only other unique behavior observed was between two different pairs of males which stood facing each other with their foretarsi overlapped and touched mouthparts or one male touched his labellum to the antennae and frons of the other male. Nonreceptive females resisted the attentions of males by head-butting; by turning swiftly towards males attempting to mount them from the rear, as is usual; and by not parting their wings and to prevent newly mounted males from grasping the females' anterolateral abdominal terga with their foretarsi.

Seasonal history.—*Procecidochares anthracina* is a univoltine, circumnata species (Headrick and Goeden 1994) on *S. californica* in southern California. The overwintering stages are first- and second-instar larvae which continue their slow, protracted development beneath insulating snow and humus as the winter progresses. When spring arrives and their host plant resumes

growth during April–May, the galls and larvae within resume their growth and development, the larvae pupariate, and the adults emerge in late summer (July–September), to mature, mate, and oviposit as described above.

Natural enemies.—Two species of chalcidoid Hymenoptera have been reared by us as parasitoids of *P. anthracina*. *Eurytoma obtusiventris* Gahan (Eurytomidae) is a solitary, larval-pupal endoparasitoid recovered from puparia that also has been reported from the tephritids, *Eurosta solidaginis* (Fitch) and *Neotephritis* (as *Tephritis*) *finalis* (Loew) (Bugbee 1967, Foote et al. 1993). *Pronotalia carlinarum* Gradwell (Eulophidae) is a gregarious puparial endoparasitoid, the only species in this genus known from North America, and a known gregarious endoparasitoid of puparia, mainly Tephritidae, but also Agromyzidae and Chloropidae (LaSalle 1994).

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LITERATURE CITED

- Bezzi, M. 1910. Restaurazione del genere *Carponymia* (Rond.) A. Costa. Bollettino del Laboratorio di Zoologia generale e agraria della R. scuola superiore d'agricoltura in Portici 5: 3–33.
- Bezzi, M. and J. S. Tavares. 1916. Alguns muscideos cecidogenicos do Brasil. Broteria (Serie Zoologica) 14: 155–170.
- Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc. Portland, Oregon.
- Bugbee, R. E. 1967. Revision of chalcid wasps of genus *Eurytoma* in America North of Mexico. Proceedings of the United States National Museum 118: 433–552.
- Doane, R. W. 1899. Notes on Trypetidae with descrip-

- tions of new species. *Journal of the New York Entomological Society* 7: 177–193, pl.
- Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. *Bulletin of the California Insect Survey* 7, 117 p.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. *Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico*. Cornell University Press, Ithaca, New York.
- Goeden, R. D. and D. H. Headrick. 1990. Notes on the biology and immature stages of *Stenopa affinis* Quisenberry (Diptera: Tephritidae). *Proceedings of the Entomological Society of Washington* 92: 641–648.
- . 1991a. Notes on the biology, hosts, and immature stages of *Tomoplagia cressoni* Aczél in southern California. *Proceedings of the Entomological Society of Washington* 93: 549–558.
- . 1991b. Life history and descriptions of immature stages of *Tephritis baccharis* (Coquillett) on *Baccharis salicifolia* (Ruiz & Pavon) Persoon in southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist* 67: 86–98.
- . 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: tephritidae) on native Asteraceae in southern California. *Proceedings of the Entomological Society of Washington* 94: 59–77.
- Goeden, R. D., D. H. Headrick, and J. A. Teerink. 1993. Life history and descriptions of immature stages of *Tephritis arizonaensis* Quisenberry (Diptera: Tephritidae) on *Baccharis sarothroides* Gray in southern California. *Proceedings of the Entomological Society of Washington* 95: 210–222.
- . 1994a. Life History and descriptions of immature stages of *Procecidochares flavipes* Aldrich (Diptera: Tephritidae) on *Brickellia* spp. in southern California. *Proceedings of the Entomological Society of Washington* 96: 288–300.
- . 1994b. Life history and description of immature stages of *Paroxyna genalis* (Thomson) (Diptera: Tephritidae) on native Asteraceae in southern California. *Proceedings of the Entomological Society of Washington* 96: 612–629.
- . 1995a. Life history and description of immature stages of *Urophora timberlakei* Blanc and Foote (Diptera: Tephritidae) on native Asteraceae in southern California. *Proceedings of the Entomological Society of Washington* 97: 780–791.
- . 1995b. Life history and descriptions of immature stages of *Valentibulla californica* (Coquillett) (Diptera: Tephritidae) on *Chrysothamnus nauseosus* (Pallas) Britton in southern California. *Proceedings of the Entomological Society of Washington* 97: 548–560.
- Goeden, R. D. and J. A. Teerink. 1996a. Life histories and descriptions of adults and immature stages of two cryptic species, *Aciurina ferruginea* (Doane) and *A. michaeli* new species (Diptera: Tephritidae) on *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. *Proceedings of the Entomological Society of Washington* 98: 415–438.
- . 1996b. Life history and descriptions of adults and immature stages of *Aciurina idahoensis* Steyskal (Diptera: Tephritidae) on *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. *Proceedings of the Entomological Society of Washington* 98: 681–694.
- . 1996c. Life history and descriptions of adults and immature stages of *Aciurina semilucida* (Bates) (Diptera: Tephritidae) on *Chrysothamnus viscidiflorus* (Hooker) Nuttall in southern California. *Proceedings of the Entomological Society of Washington* 98: 752–766.
- . 1997. Notes on life histories and descriptions of adults and immature stages of *Procecidochares kristineae* and *P. liseae* new spp. (Diptera: Tephritidae) on *Ambrosia* spp. in southern California. *Proceedings of the Entomological Society of Washington* 99: 67–88.
- Green, J. F., D. H. Headrick, and R. D. Goeden. 1993. Life history and description of immature stages of *Procecidochares stonei* Blanc & Foote on *Viguiera* spp. in southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist* 69: 18–32.
- Headrick, D. H. and R. D. Goeden. 1990. Description of the immature stages of *Paracantha gentilis* (Diptera: Tephritidae). *Annals of the Entomological Society of America* 83: 220–229.
- . 1991. Life history of *Trupanea californica* Malloch (Diptera: Tephritidae) on *Gnaphalium* spp. in southern California. *Proceedings of the Entomological Society of Washington* 93: 559–570.
- . 1993. Life history and description of immature stages of *Aciurina thoracica* (Diptera: Tephritidae) on *Baccharis sarothroides* in southern California. *Annals of the Entomological Society of America* 86: 68–79.
- Headrick, D. H., R. D. Goeden, and J. A. Teerink. 1995. Life history and description of immature stages of *Euaestha stigmatica* Coquillett (Diptera: Tephritidae) on *Ambrosia* spp. (Asteraceae) in southern California. *Annals of the Entomological Society of America* 88: 58–71.
- . 1996. Life history and description of immature stages of *Dioxyna picciola* (Bigot) (Diptera: Tephritidae) on *Coreopsis* spp. (Asteraceae) in southern California. *Proceedings of the Entomological Society of Washington* 98: 332–349.
- Knio, K. M., R. D. Goeden, and D. H. Headrick. 1996. Descriptions of immature stages of *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae). *Annals of the Entomological Society of America* 89: 1–11.
- LaSalle, J. 1994. North American genera of Tetrasti-

- chinae (Hymenoptera: Eulophidae). *Journal of Natural History* 28: 109–236.
- Munz, P. A. 1974. *A Flora of Southern California*. University of California Press, Berkeley.
- Silverman, J. and R. D. Goeden. 1980. Life history of a fruit fly, *Procecidochares* sp., on the ragweed *Ambrosia dumosa* (Gray) Payne, in southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist* 56: 283–288.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology, Occasional Papers 19: 1–72.